

Reproductive Biology of the African Lungfish *Protopterus annectens annectens* (Owen, 1839) in the Mono River Basin of Benin, West Africa

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ABSTRACT

In the Mono River basin, the African lungfish, *Protopterus annectens annectens* is found in temporary ponds. This species is of great economic interest because of its high contribution to fisheries. As a result, this study aims at documenting some aspects of its biology. A monthly sampling was conducted during the exploitation period (the rainy season, i.e., July through October 2015). A total of 281 females and 215 males bought from local fishermen were used for the study of reproductive biology and to generate a length-weight relationship. The results show that the specimens' growth is of the negative allometric type in both males and females. Mean sex ratio (1:0.77) favored females and was significantly different from a 1:1 ratio. Size at first sexual maturity was 29.6 and 30.4 cm total length in females and males, respectively. Frequency distribution of ovum diameter is bimodal, suggesting split-spawning during the breeding season. Absolute fecundity ranged from 447 to 1,200 eggs, while relative fecundity ranged from 4 to 9 eggs per gram of body weight.

Keywords: Length-weight relationship, Mono River, Protopteridae, Reproduction, West Africa

INTRODUCTION

Fish is one of the most traded staple foods in the world. It is a vital source of protein and essential nutrients, especially for many poor people (FAO, 2016). The use for human consumption has increased over the years as a result of the continuous increase in human population. Consequently, the state of stocks worldwide is declining at an alarming rate due especially to poor management of fisheries resources (Jamu and Ayinla, 2003; Akpaniteaku *et al.*, 2005). Lalèyè *et al.* (1997) and Lederoun *et al.* (2016b) have reported that in many aquatic ecosystems in Benin, for example, large-bodied fish have become very scarce in the fisheries. However, the population traits of targeted fishery species have been very poorly studied (Lederoun *et al.*, 2016b).

The family Protopteridae belongs to the subclass Sarcopterygii, which used to be represented by a number of forms in prehistoric times, with just one species still in existence today in Australia, another in Amazonia, and four *Protopterus* species (*Protopterus dalloi*, *P. aethiopicus*, *P. annectens* and *P. amphibius*) in Africa (Lévêque and Paugy, 2003; Boden, 2007; Nelson *et al.*, 2016). Poll (1961) subdivided *P. annectens* into two subspecies: *P. annectens brienii* and *P. annectens annectens*. The first is encountered in the Congo, Zambezi, Cubango, and Okavango basins. The second, the subject of this work, is found in the swamps of West Africa. In Benin, in particular, *P. a. annectens* is found in the Pendjari (Ahouansou Montcho, 2011; Moritz and Lalèyè, 2019), Ouémé (Lalèyè *et al.*, 2004; Montchowui *et al.*, 2007), and Mono basins (Paugy and Bénèch, 1989; Lederoun *et al.*, 2018).

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In the Mono basin, on which this investigation focuses, *Protopterus annectens annectens* dwells in temporary ponds, which are tightly enclosed by dense vegetation and which are periodically flooded. During the dry season, this fish sinks into the moist ground and secretes a mucus-based cocoon which envelops it and within which it lives until the next occurrence of water. It is a taxon of great economic interest because it makes up a high percentage of the total catch by the fisheries industry. In the lower valley of the Mono River, for example in the swamps around the city of Athiémé (approx. 06° 33'N – 01° 41'E), it represents more than 80% of the catch meant for sale when water has returned and the land is submerged again. The species is exploited with traditional traps during the annual floods (July to October), and the only reliable statistics available in recent years (1990–2000) for portions of the basin (Coastal lagoon of Grand-Popo, Lakes Doukon, Toho and Togbadji) indicated an average of 2.3 tonnes per year (Department of Fisheries of Benin, unpublished data). However, this species does not receive the same attention from scientists as do other abundant species which are caught in the same basin, such as the Cichlids *Sarotherodon melanotheron melanotheron* (Lederoun *et al.*, 2015) and *Sarotherodon galilaeus galilaeus* (Lederoun *et al.*, 2016a). In fact, these species have recently been investigated in the Mono basin. However, to best manage the fish resources of a given environment, it is essential to identify the species using that environment as habitat and to be informed about their abundance, distribution, biology and ecology (Lalèyè, 2006; Al-Barwani *et al.*, 2007; Montchowui *et al.*, 2009, 2011; Lederoun *et al.*, 2016a). Data relative to *P. a. annectens* biology in the Mono River basin are currently non-existent. The present work, which attempts to fill this void, addresses some of the aspects of the reproductive biology of this species. Specifically, we investigated the size frequency distribution, length-weight relationship, condition factor, sex ratio, size at first maturity and fecundity in the *P. a. annectens* population of the Mono River. The results obtained will be useful for stock assessment and fisheries management.

MATERIALS AND METHODS

Study area

This study was conducted in the Djonnougui swamps (located roughly at 06° 33'N - 01° 41'E) in Athiémé, a locality on the Benin side of the Mono basin; the Mono basin being a coastal basin straddling the border between Benin and Togo (Figure 1). The Mono River is approximately 360 km long and has its source in the Koura Hills in the city of Aledjo (approx. 9°21' N - 01°27' E) in northwestern Benin. It drains a 25,000 km² watershed between 6°10' and 9°00' N latitudes and 0°30' and 1°50' E longitudes (Lederoun *et al.*, 2016b, 2018). In the east, it runs into the coastal Grand Popo and Lake Ahémé lagoon system of Benin, while to the west, it runs into the Lake Togo and Vogan Lagoon system in the Republic of Togo. Its connection with the Togolese lagoon system is facilitated by the Gbaga Lagoon located on the right bank (Figure 1).

Since the construction of a hydroelectric dam on its main channel in 1987, the Mono River has been divided into three distinct ecological zones: the upstream zone, the downstream zone, and the Nangbeto reservoir. It overflows greatly during high-water periods and floods a vast area downstream of the dam (the lower Mono Valley) that includes the Mono lakes and the Djonnougui pond. The latter is an environment totally enclosed by dense vegetation and which is periodically flooded. The times it gets submerged by water are dependent on the two rainy seasons that are characteristic of southern Benin's climate: an early rainy season that runs from mid-March to mid-July and a late rainy season that runs from mid-September to November. These rainy seasons are separated by two dry seasons: a short one from mid-July to early September, and a long one from early December to mid-March (Lederoun *et al.*, 2018).

Sampling method

Monthly sampling was conducted during the *Protopterus annectens annectens* fishing season (July to October 2015). The fish were taken directly from local fishermen who mainly use traditional

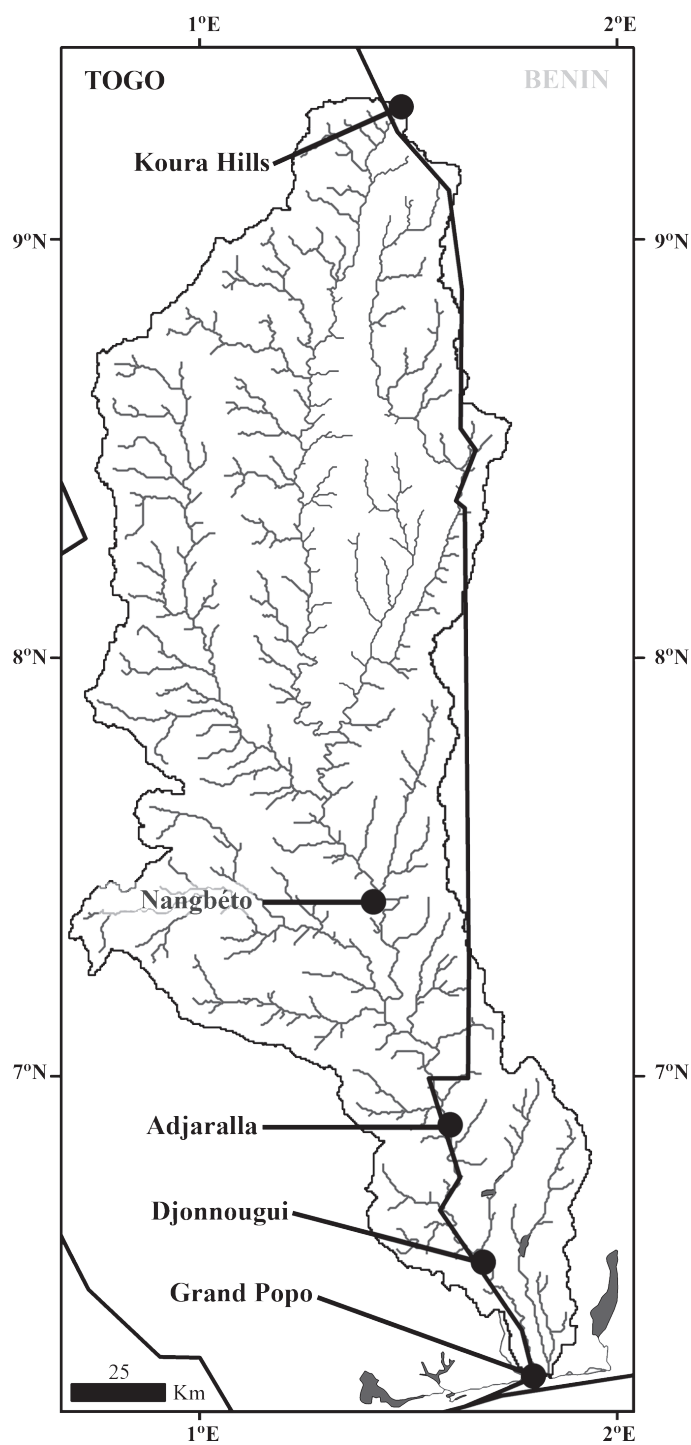


Figure 1. Map showing locations of Djonnougui and Athiémé in the Mono River basin, Benin.

traps with palm nuts (*Elaeis guineensis*) or maize flour (*Zea mays*) turned into dough with hot water and used as bait. They were killed on the spot by choking and then kept iced until transport to the lab, where they were measured and weighed. The fish were measured for total length (TL) and weighed individually (total and eviscerated weight) to an accuracy of 0.01 g. Sex was determined after dissection and macroscopic examination of the gonads. Stage of maturity was assessed based on the maturity scale (5 levels) established by Brown-Peterson *et al.* (2011). All males or females from stages III to V were considered mature. Gonads were collected and weighed to the nearest 0.01 g using an electronic precision balance. Five to ten stage-IV ovaries, collected each month, were fixed in alcohol for the determination of fecundity.

Data processing

Length-weight relationship

The relationship between total length (TL) and total weight (BW) was established using the equation $BW = aTL^b$ (Le Cren, 1951), where BW is body weight in g, TL is total length in cm, a is the intercept, and b is the slope of the linear regression. The relationship was established in this study for males, females and both sexes. The 95 % confidence limits for b were assessed using Statview (v. 5.0.1, SAS Institute). As described by Lederoun *et al.* (2016b), Student t-test was conducted following Sokal and Rohlf (1987) to check whether b is significantly different from the value 3. ANCOVA was used to test for difference in the bi-logarithmic weight-length relationships between sexes. Differences were considered significant at 5% ($p < 0.05$).

Size at first maturity

Size at first maturity (L50) was estimated using the expression $P = e^{(\alpha + \beta TL)} / (1 + e^{(\alpha + \beta TL)})$, where P is the percentage of sexually mature individuals, α and β are intercept and slope of the logistic regression, respectively, and TL is the total length. The logarithmic transformation of the previous formula corresponds to the following: $\ln[P/(1 - P)] = \alpha + \beta TL$ and, by substituting $P = 50\%$ in the previous

equation, L50 is obtained by the formula: $L50 = -\alpha/\beta$. All individuals at maturity stages 3 to 5 were considered to have active gonads. Likelihood-ratio tests were performed to detect differences in L50 values between sexes (Lederoun *et al.*, 2016b). Statview (v. 5.0.1, SAS Institute) was used to calculate the estimated proportion of mature fish and coefficients α and β in the model.

Condition factor

Condition factor (K) was estimated using the equation $K = BW/TL^b \times 100$ (Tesch, 1971), where BW and TL are the variables used to determine the Weight-Length relationship. Non-parametric Kruskal-Wallis test and Mann-Whitney U-tests were performed with PAST 3.26 software to test the difference of the results among all months and between two months, respectively. Differences were considered significant at 5 % ($p < 0.05$).

Ovarian structure and fecundity

To determine the ovarian structure at the time of oviposition, ovarian oocytes collected from females at stage IV were measured, after dissociation of ovarian tissue, using Vista Metrix 1.36 software. The ovarian structure was determined from frequency histograms that were designed using data from oocyte measurements. The different groups of oocytes (immature and mature) were classified. Fecundity was determined by systematic counting of mature oocytes in the removed ovaries. From the data obtained, absolute fecundity is determined and is equivalent to the number of mature oocytes per ovary. Relative fecundity is calculated by dividing absolute fecundity by the total weight of the fish (Montchowui *et al.*, 2007).

RESULTS

General structure by fish size

The overall distribution of population size frequencies from *Protopterus annectens annectens* sampled during the study period is shown in Figure 2. The distribution is unimodal. Recorded extreme sizes are 14.3 and 57.5 cm.

Length-weight relationship

Table 1 presents the results of an analysis of the body weight/total body length relationship in *Protopterus annectens annectens* for males, for females, and for both sexes. Males were in the range of 20.1 - 46.0 cm TL at body weights of 38.5 - 542.3 g, while females were in the range of 14.3 - 41.8 cm TL at body weights of 11.7 - 323.0 g. Regardless of the sex, the allometric coefficient was significantly lower than 3 ($t_s = -3.223$, -7.159 and -7.228 , respectively for males, females and both sexes). This result reflects negative allometric growth, meaning that an increase in total length is proportionally greater than an increase in weight.

Condition factor

Mean condition factor values ranged from 0.86 ± 0.12 to 1.10 ± 0.18 for males and from 2.70 ± 0.42 to 3.54 ± 0.64 for females (Table 2). The lowest values were obtained in August after flooding of the ponds and the highest in October at the start of low flows. There is a highly significant difference

between the condition factor for males and females (Mann-Whitney test, $p < 0.001$). For males, the difference in values among months is highly significant (Kruskal-Wallis test, $p < 0.001$). Differences between the condition factors of July-August, August-September and August-October are highly significant (Mann-Whitney test, $p < 0.001$). They are significant (Mann-Whitney test, $p < 0.05$) between September and October (Table 3). For females, variation in the condition factor among the different months is highly significant (Kruskal-Wallis test, $p < 0.001$). Differences between the condition factors of July-August, August-September and August-October are also highly significant (Mann-Whitney test, $p < 0.001$) (Table 3).

Sex ratio

Of the 496 mature specimens, 281 (56.28 %) were females and 215 were males, giving a sex ratio of 1 female for 0.77 males (1:0.77). This sex ratio is significantly different from the theoretical sex ratio of 1:1 ($\chi^2 = 8.78$, $p < 0.05$). A preponderance of females over males was observed throughout the season (Table 4).

Table 1. Descriptive statistics and estimated length-weight relationship parameters ($BW = a TL^b$) for *Protopterus annectens annectens* collected from the Mono basin. A-: negative allometric growth; a: intercept; b: allometric growth coefficient = slope; BW: body weight; CL: confidence limit; Min: minimum; Max: maximum; N: sample size; r^2 : coefficient of determination; TL: total length.

| Sex | N | TL (cm) | | BW (g) | | Regression parameters | | | | | Growth |
|---------------|-----|-----------|----------------|------------|------------------|-----------------------|-------|---------|-------------|-------|--------|
| | | Min-Max | mean \pm SD | Min-Max | mean \pm SD | a | b | SE of b | 95% CL of b | r^2 | |
| Male | 207 | 20.1-46.0 | 29.8 \pm 4.6 | 38.5-542.3 | 117.2 \pm 65.0 | 0.009 | 2.755 | 0.076 | 2.605-2.950 | 0.864 | A- |
| Female | 275 | 14.3-41.8 | 31.1 \pm 4.1 | 11.7-323.0 | 129.5 \pm 48.4 | 0.031 | 2.413 | 0.082 | 2.251-2.575 | 0.758 | A- |
| Male + Female | 482 | 14.3-46.0 | 30.5 \pm 4.3 | 11.7-542.3 | 124.2 \pm 56.4 | 0.017 | 2.588 | 0.057 | 2.477-2.699 | 0.812 | A- |

Table 2. Condition factor for *Protopterus annectens annectens* males and females in the Mono basin.

| Month | Sample size | | Condition factor | | Average condition factor (\pm SD) | |
|-----------|-------------|--------|------------------|-----------|--------------------------------------|--------------------|
| | Male | Female | Male | Female | Male | Female |
| July | 52 | 68 | 0.73-1.70 | 2.13-4.94 | 1.03 (\pm 0.16) | 3.46 (\pm 0.47) |
| August | 76 | 108 | 0.63-1.16 | 2.02-4.89 | 0.86 (\pm 0.12) | 2.70 (\pm 0.42) |
| September | 66 | 68 | 0.72-1.33 | 2.29-4.24 | 0.99 (\pm 0.15) | 3.38 (\pm 0.45) |
| October | 14 | 32 | 0.89-1.59 | 1.90-4.84 | 1.10 (\pm 0.18) | 3.54 (\pm 0.64) |

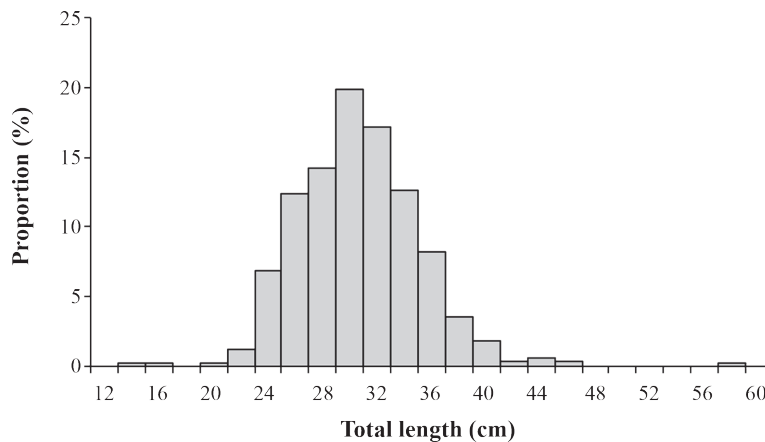
Table 3. Summary of the Mann-Whitney test on *Protopterus annectens annectens* male and female condition factor variation within the Mono basin based on the month of sampling (n=4).

| Month | July | | August | | September | | October | |
|-----------|------|--------|--------|--------|-----------|--------|---------|--------|
| | Male | Female | Male | Female | Male | Female | Male | Female |
| July | 1 | 1 | ** | ** | ns | ns | ns | ns |
| August | | | 1 | 1 | ** | ** | ** | ** |
| September | | | | | 1 | 1 | * | ns |
| October | | | | | | | 1 | 1 |

Note: Note: ns=non-significant difference; M=male; F=Female; *=significant difference ($p<0.05$); **=highly significant difference ($p<0.001$).

Table 4. Monthly distribution of maturity stages and sex ratio of *Protopterus annectens annectens* in the Mono basin.

| Month | Sex of fish | Gonad maturity stages | | | | | N | Sex ratio (F:M) | χ^2 |
|-----------|-------------|-----------------------|----|-----|-----|----|-----|-----------------|----------|
| | | I | II | III | IV | V | | | |
| July | M | - | 2 | 30 | 18 | 2 | 52 | 1:0.76 | 2.13 |
| | F | - | - | - | 63 | 5 | 68 | | |
| August | M | 2 | 10 | 37 | 24 | 4 | 77 | 1:0.71 | 5.19* |
| | F | - | 1 | 5 | 70 | 32 | 108 | | |
| September | M | 8 | 13 | 22 | 15 | 8 | 66 | 1:0.97 | 0.03 |
| | F | - | 2 | 3 | 19 | 44 | 68 | | |
| October | M | 1 | - | 1 | 17 | 1 | 20 | 1:0.54 | 5.07* |
| | F | - | 3 | 1 | 33 | - | 37 | | |
| Total | M | 11 | 25 | 90 | 74 | 15 | 215 | 1:0.77 | 8.78* |
| | F | - | 6 | 9 | 185 | 81 | 281 | | |

Figure 2. Size frequency distribution of *Protopterus annectens annectens* in the Mono basin.

Size at first maturity

In the Mono basin, 50 % of male and female *Protopterus annectens annectens* were sexually mature at 29.6 and 30.4 cm, respectively (Figure 3). There was no significant difference in the estimated size at maturity between males and females ($p = 0.8762$).

Ovary structure and fecundity

The diameter frequency distribution of stage-IV oocytes is shown in Figure 4. Oocyte size varied between 0.175 and 7.51 mm, with an average of 2.81 ± 1.57 mm. Ovarian structure analysis reveals the presence of two oocyte peaks (Figure 4). Group I oocytes (i.e., the left peak), which shall generate new eggs, were roughly 0.175 and 2.6 mm in diameter, respectively. Group II oocytes, quite remarkable for their size (2.7 to 7.51 mm), were easily retrieved with manual pressure. This is the group holding the more advanced oocytes which will be laid in the next spawning season. Average egg diameter at the time of spawning was 4.03 mm (± 0.80). Fecundity was estimated using group II oocytes and 32 female gonads all at stage IV of sexual maturity (27.5 to 36.4 cm TL, 106.7 to 202.0 g BW). The average gonad weight of the females was 28.79 ± 6.25 g (31.2 ± 2.1 cm TL, 146.42 ± 24.43 g BW). Mean absolute fecundity was 809 ± 197 eggs and relative fecundity was 6 ± 1

eggs per gram of body weight. Relative fecundity ranged from 4 to 9 eggs per gram of body weight. The observed maximum absolute fecundity was 1,200 eggs in a gonad weighing 44.2 g in a female whose size was 36.4 cm TL for a total weight of 198.2 g. The observed absolute minimum fecundity was 447 eggs in a gonad weighing 19.2 g in a female whose size was 31.4 cm TL for a total weight of 121.8 g. There are linear relationships between absolute fecundity and total female weight, and between absolute fecundity and female gonad weight (Figure 5).

Because the oocytes were quite large and easily identified with the naked eye, we were able to obtain an average total number of oocytes (Groups I and II) of $1,261 \pm 235$. The maximum number of oocytes was 1,723 in a female whose size was 36.4 cm TL for a total weight of 198.2 g and whose gonads weighed 44.2 g. The minimum number was 818 in a gonad weighing 19.2 g in a female whose size was 31.4 cm TL and with a total weight of 121.8 g. A linear relationship is clearly observed between the total number of oocytes present in the ovary and the weight of the ovary (Figure 6). In the 32 females examined, the average number of oocytes with a diameter between 0.175 and 2.6 mm (Group I) was 453 ± 90 . Overall, $63.57 \pm 6.34\%$ of the oocytes (Group II, Figure 4) present in the ovary were mature at the time of spawning.

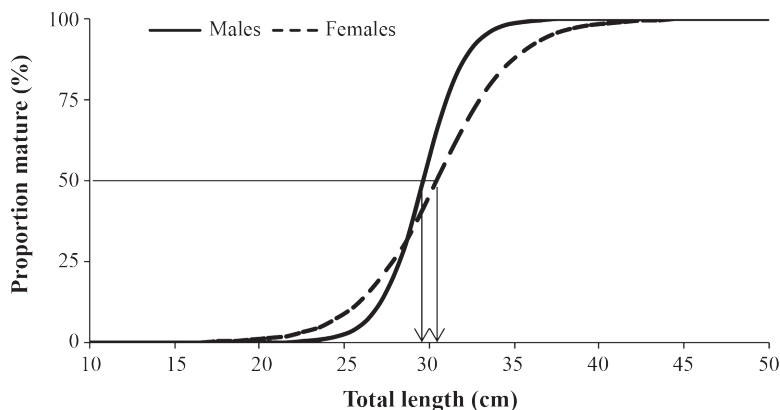


Figure 3. Estimated size at first maturity of *Protopterus annectens annectens* males and females in the Mono basin.

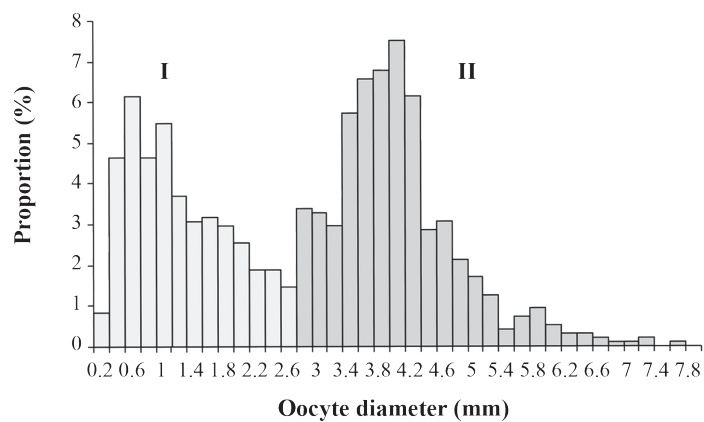


Figure 4. Oocyte frequency distribution of *Protopterus annectens annectens* before spawning (stage IV).

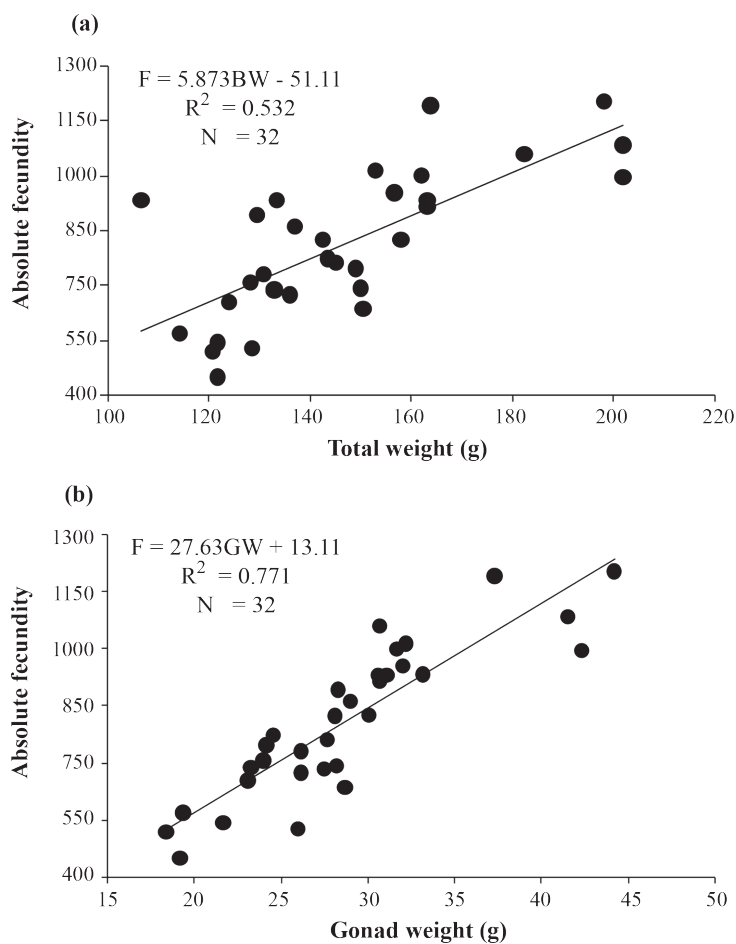


Figure 5. Relationships between fecundity and total weight (a) and between fecundity and ovary weight (b) of *Protopterus annectens annectens*.

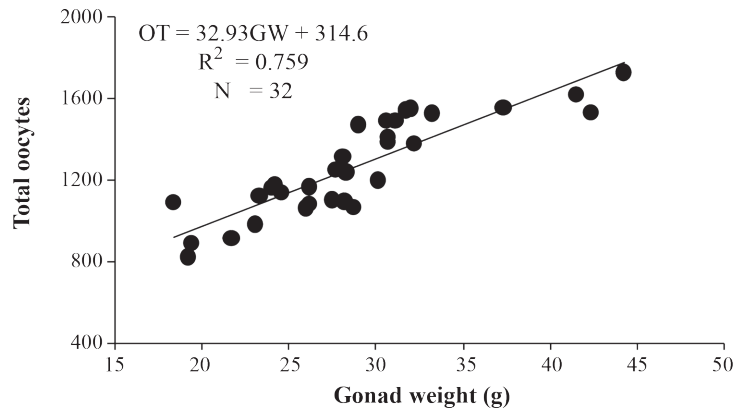


Figure 6. Relationship between total oocytes and ovary weight of *Protopterus annectens annectens*.

DISCUSSION

In this study, the smallest *Protopterus annectens annectens* specimen measured 14.3 cm TL and the largest was 46.0 cm TL. This gives a wide variation in size, which indicates that the sampling covered both juveniles and adults. The use of baited traditional traps made of 6-, 8- and 10-mm mesh size explains this result.

The length-weight relationship (LWR) is an important factor in the biological study and stock assessment of fishes (Kohler *et al.*, 1995; Braccini *et al.*, 2006; Lederoun *et al.*, 2016a). The slope (b) of the relationship varies between 2 and 4 but is often close to 3. It expresses the relative shape of the body of a fish. If $b = 3$, the growth is isometric. If $b \neq 3$, the growth is allometric. A value $b > 3$ indicates better growth in weight than in length and vice versa if $b < 3$. The estimated slope values (b) of 2.755 in males, 2.413 in females and 2.588 in both sexes show that *Protopterus annectens annectens* exhibits a negative allometric growth. This indicates that the rate of increase in body length was not proportional to the increase in body weight. This result corroborates those of Adeyemi (2010), who obtained a b coefficient of 2.553 for both sexes in the Idah area of the Niger River in Nigeria. But this result is different from those of Oniye *et al.* (2006), who obtained b coefficients of 3.12 and 3.22 in males and females, respectively, at the Jachi dam in Nigeria. Divergence in results

could be due to the types of habitats surveyed (Konan *et al.*, 2007), to the number of samples, or to the length and weight taken into account for calculating the LWR, with the b coefficient increasing with the length of the fish. However, sex, season, stage of maturity, water quality, food availability and sampling method may also explain the variation observed in b values between ecosystems (Tesch, 1971; Wootton, 1990; Fontaine *et al.*, 1996; Saillant *et al.*, 2001; Lalèyè, 2006; Konan *et al.*, 2007; Hossain *et al.*, 2009). In Lake Baringo, Kenya, *P. aethiopicus* has positive allometric growth, with a slope of 3.52 for both sexes (Mlewa and Green, 2004), which indicates better growth in weight.

The sex ratio obtained in this study (1:0.77) is in favor of females and is significantly different from 1. This result can be explained by the parental care provided by males to the young. In fact, the male monitors the nests until the young reach 30 to 35 mm in size (Thys van den Audenaerde and Snoeks, 1997). This could explain their lower number in the catches. A sex ratio (1:1.64) in favor of females was similarly obtained for *Protopterus aethiopicus* in Lake Baringo (Mlewa and Green, 2004).

Mean condition factor values ranged from 0.86 to 1.10 in males and from 2.70 to 3.54 in females. Obtained values are higher than those of Adeyemi (2010), who found 0.23 to 0.76 for both sexes of the same species in the Idah area of the Niger River

in Nigeria. This result shows that fish in the Mono basin are in a more favorable environment. The difference between males and females in this study may be attributed to the use of total weight in the calculations, which includes the weight of the stomach's content and the weight of the gonads. This is because the stomach's content represents an important proportion of the total body weight. On the other hand, gonads are likely to significantly alter the weight of females during the breeding season (Lederoun *et al.*, 2016a). Okafor (2011) investigated this condition factor parameter in a wet season (April to October) in the Anambra River at Otuocha (Nigeria) without taking into account the weight of the gonads. He found that, in females, the mean K values were from 1.0 to 2.0 (mean 1.7 ± 0.7), while the values ranged from 0.6 to 1.7 (mean 1.3 ± 0.7) in males. This shows that the weight of the female gonads considerably affects the total weight of the fish and, thus, determines the significant difference observed between the male and female K values. The values obtained in this study are higher than those obtained for *Protopterus aethiopicus* from Lake Baringo, which ranged from 0.72 to 1.58 for both sexes during the same study period (Mlewa and Green, 2004).

In the Mono basin, *Protopterus annectens annectens* matures at 29.6 cm TL in males and 30.4 cm in females. The difference in size of sexual maturity has already been observed in many fish species (Mlewa and Green, 2004; Montchowui *et al.*, 2007; Lederoun *et al.*, 2015, 2016b) and is probably due to asexual dimorphism of growth in the species (Montchowui *et al.*, 2007). In Lake Baringo, size at first maturity in *P. aethiopicus* was 82-88 cm TL in males and 70-76 cm TL in females (Mlewa and Green, 2004).

The absolute mean fecundity was 809 ± 197 eggs and the average relative fecundity was 6 ± 1 eggs per g of body weight. Thys van den Audenaerde and Snoeks (1997) reported 2,000-2,500 mature eggs for *Protopterus aethiopicus*. In Lake Baringo, an average fecundity of 10,711 eggs per female was reported for this species (Mlewa and Green, 2004). In *Protopterus dolloi*, the only Protopteridae species

that reproduces in the dry season, during low water flows, the female can hold 300 eggs (Thys van den Audenaerde and Snoeks, 1997).

Protopterus annectens annectens breeds when the floodplain is flooded in the lower valley of the Mono basin between July and October. In the Orie River and its floodplain in Nigeria, Otuogbai *et al.* (2002) reported that the species breeds from July to August. This seasonal breeding behavior differs from that observed in *Protopterus aethiopicus* in Lake Baringo. Indeed, marbled lungfish (*P. aethiopicus*) in this lake breed throughout the year with no evidence of synchronized breeding with seasons (Mlewa and Green, 2004). This is proven by the presence of different egg sizes in the ovaries of mature females and by the occurrence of females in breeding condition (sexual maturity stages III-IV) throughout the year (Mlewa and Green, 2004).

The average egg diameter at the time of egg laying in the Mono River was 2.81 ± 1.57 mm. In the Orie River and its floodplain in Nigeria, the mean diameter at the time of reproduction was 1.99 ± 0.60 mm (Otuogbai *et al.*, 2002). Ovum diameter frequency distribution was bimodal (large oocytes), suggesting split spawning. Otuogbai *et al.* (2002) also found a structure that suggests that the fish spawn more than once during the spawning period. Thys van den Audenaerde and Snoeks (1997) pointed out that the species builds nests 50-100 cm deep in the lowlands during breeding and that in these nests there are young individuals at different stages of development. This either suggests that the female lays her eggs several times a few days apart or that several females lay their eggs in the same nest. The frequency distribution of diameters obtained in this study shows that the same female lays eggs more than once in the same nest during the breeding season (rainy season). However, it is not impossible that several females use the same nest at the same time. Almost half of the oocytes reach maturity at the time of egg-laying. There is a large amount of immature oocytes at the time of egg-laying, and these will generate new eggs for the next cycle.

CONCLUSION

Protopterus annectens annectens exhibits negative allometric growth in the Mono River basin. It is a large-bodied fish that has a sex ratio in favor of females because of the parental care provided by males to the young. This species has split spawning and relatively low fecundity. The present study, by its results, constitutes an important database for further population assessments of the species.

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